

AN EXAMINATION OF THE NORTH AMERICAN APHID SPECIES
CURRENTLY PLACED IN *OVATUS* VAN DER GOOT (HEMIPTERA:
APHIDIDAE) WITH THE DESCRIPTION OF A NEW GENUS

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Abstract.—The current placement in *Ovatus* of four endemic North American aphid species is critically examined. Results of cladistic analyses clearly indicate that these four species are not congeneric with Palearctic *Ovatus* and that they are more closely related to *Myzus* Passerini. Cladistic evidence is provided to justify the erection of a new genus, *Abstrusomyzus* **n. gen.**, for the four endemic North American species formerly placed in *Ovatus*. This resulted in four new combinations: *Abstrusomyzus leucocrini* (Gillette & Palmer) **n. comb.**, *Abstrusomyzus phloxae* (Sampson) **n. comb.**, *Abstrusomyzus reticulatus* (Heie) **n. comb.**, and *Abstrusomyzus valuliae* (Robinson) **n. comb.** Information on each of the four species is compiled and presented. Illustrations are provided, along with a key to the species of the new genus and notes on the single remaining species of *Ovatus* in North America, *Ovatus crataegarius* (Walker).

Key Words: polyphagy, *Myzus*, *Ovatus*, new genus, cladistics

Most aphids are extremely host specific, feeding on one or a few species of plants that are usually closely related (Eastop 1973). Many of the most pestiferous aphids known differ dramatically from this normal pattern by being polyphagous on plants in widely divergent families. Well-known polyphagous pests include the green peach aphid [*Myzus persicae* (Sulzer)], the potato aphid [*Macrosiphum euphorbiae* (Thomas)], and the cotton aphid (*Aphis gossypii* Glover). These aphids can cause serious problems even when they feed on a crop in low numbers, since they can transmit plant viruses between their phylogenetically disparate host plants. Very few polyphagous aphids are not pests. Given the fact that many of the most serious pest aphids are polyphagous, it is important to study newly-discovered cases of polyphagy in aphids. As po-

lyphagous aphids are likely to some day become pests, prior knowledge of their biology, taxonomy, and evolution will facilitate an effective reaction to their emergence as pests.

Ovatus phloxae (Sampson) is one of the few polyphagous aphids that so far is not a pest. It was described in 1939 from *Phlox subulata* from Berkeley, California. Since then it has been found on eighteen plants in fourteen families (Table 1). It has been collected in most regions of the United States and probably occurs in most temperate parts of North America. Most plants on which this aphid has been found have a basal rosette of leaves, or tend to be prostrate. The aphid usually lives in the crown or on the lower leaves. It is possible that this species is more habitat specific than host specific, much as in *Rhopalosiphum nymphaeae* (L.), which

Table 1. Host plants and distributions for five species heretofore placed in *Ovatus*.

Aphid Species	Host Plants	Distribution	
<i>Ovatus crataegarius</i> (Walker)	Rosaceae	Almost worldwide, with a Palearctic origin	
	<i>Crataegus</i> spp.		
	<i>Cydonia</i> spp.		
	<i>Malus</i> spp.		
	Lamiaceae		
	<i>Mentha</i> spp. some other Lamiaceae		
<i>Ovatus leucocrini</i> (Gillette & Palmer)	Liliaceae <i>Leucocrinum montanum</i>	Colorado	
<i>Ovatus phloxae</i> (Sampson)	Apocynaceae	Canada: British Columbia	
	<i>Apocynum androsaefolium</i> <i>Apocynum</i> sp.		
	Asteraceae	U.S.A.:	
	<i>Achillea</i> sp.		California
	<i>Agoseris</i> sp.		Colorado
	<i>Centaurea</i> sp.	Maryland	
	Brassicaceae	Mississippi	
	<i>Capsella hursa-pastoris</i>	Nebraska	
	Caryophyllaceae	Oregon	
	<i>Cerastium vulgatum</i> <i>Stellaria crista</i>	Pennsylvania	
	Cyperaceae	Utah	
	<i>Carex densa</i>	Virginia	
	Fabaceae		
	<i>Trifolium</i> sp.		
	Hydrophyllaceae		
	<i>Phacelia nemoralis</i>		
	Liliaceae		
	"Lilies"		
	Plantaginaceae		
	<i>Plantago major</i>		
	Polygonaceae		
<i>Polygonum paronychia</i>			
Ranunculaceae			
<i>Ranunculus</i> sp.			
Polemoniaceae			
<i>Phlox subulata</i>			
Rubiaceae			
<i>Galium</i> sp.			
Violaceae			
<i>Viola</i> sp.			
<i>Ovatus reticulatus</i> Heie	Oxalidaceae <i>Oxalis ?stricta</i>	North Carolina	
<i>Ovatus valuliae</i> (Robinson)	Rosaceae <i>Fragaria vesca</i>	Manitoba	

feeds widely on aquatic and semiaquatic plants. If this were true, *O. phloxae* could emerge at any time as a pest of a crop with an appropriate growth habit. Therefore a study of North American *Ovatus* was undertaken to provide needed information re-

garding *O. phloxae* and three closely related endemic North American aphids currently placed in *Ovatus*. The relationship of these four species to Palearctic *Ovatus* is examined using cladistics, and a new genus is proposed for them based on these analyses.

MATERIALS AND METHODS

Most specimens studied are housed in the National Collection of Aphidoidea (USNM, located at the Systematic Entomology Laboratory, USDA, Beltsville, Maryland, USA). Others were obtained on loan from The Natural History Museum, London (BMNH); Agriculture Canada, Vancouver, British Columbia (UBC); University of California, Berkeley (UCB); and Oregon State University, Corvallis (OSU).

Aphids were mounted on microscope slides in Canada balsam or Hoyer's medium, and observed under phase contrast microscopy. Terminology follows Miyazaki (1987). Drawings were made by the first author using a camera lucida.

Cladistic analyses were performed using PAUP 3.1.1 (Swofford 1993) and MacClade 3.01 (Maddison and Maddison 1992) on 23 taxa using 25 characters. Apterous and alate viviparae were included in the character analysis, supplemented by one character of the first instar nymph. All characters were treated as unordered.

Ovatus van der Goot

Ovatus has most recently (Remaudière and Remaudière 1997) been used for fourteen *Myzus*-like aphids, which generally migrate between Pomoidea and various Lamiaceae, or are monoecious on either of these groups. Nine of the fourteen species fit this pattern of host plant association. One exception is the single member of the subgenus *Ovatoides*, *Ovatus (Ovatoides) inulae* (Walker). This species feeds on Asteraceae and differs morphologically from most *Ovatus* by the nearly complete lack of spinulation on the head and first two antennal segments, and the long, setose ultimate rostral segment. The other four species that do not conform with the Pomoidea/Lamiaceae host plant association are the four endemic North American species [Table 1, excluding *Ovatus crataegarius* (Walker)]. These species feed on herbs from a diverse set of plant families, and none of them is known from

Pomoidea or Lamiaceae. Morphologically these species differ from most Palearctic *Ovatus* by the dark bars and blotches on the abdominal tergum of the alate vivipara (Figs. 17, 18), first tarsal chaetotaxy of 3,3,2, and the peculiarly shaped siphunculus (Figs. 9–12).

The first to place one of these species in *Ovatus* was Hille Ris Lambers (1966), who transferred *Phorodon phloxae* to *Ovatus* without any explanation. Heie (1972) described *Ovatus reticulatus*, and Eastop and Hille Ris Lambers (1976) transferred *Myzus leucocrini* Gillette and Palmer and *Myzus valuliae* Robinson without explanation. The obviously close relationship among these four species dictated that they be placed together in the same genus, but their morphological and biological differences from Palearctic *Ovatus* causes doubt about their current generic placement.

CLADISTIC ANALYSES

This study attempts to determine whether the four North American species currently placed in *Ovatus* will cluster together, and whether they will form their own group, form a part of *Ovatus*, or fall within another genus. Doing this requires that the cladistic analysis include several species from one or more genera to which the species in question might be more closely related than they are to *Ovatus*. These cladistic analyses are meant to explore the proper generic placement of the four endemic North American species currently placed in *Ovatus* and are not meant to resolve species-level issues for the other aphids included in the analysis.

Choice of appropriate comparative groups for a test of the proper placement of the four endemic North American species is particularly troublesome in the case of *Ovatus* for at least three reasons. First, the fact that the analysis deals with aphids presents problems in itself (see Jensen 1997 for some discussion of this issue). Aphids are highly progenetic *sensu* Gould (1977), and because of their conservative morphology most genera lack apomorphic characters. Instead, there is

essentially a large pool of characters that occur across a wide range of aphid taxa, and many genera are recognized on the basis of a unique combination of these characters. Aphid genera are also frequently defined by the absence of one or more characters typical in genera to which they are most similar morphologically. These facts, in combination with the lack of work on the evolution of the commonly used aphid characters, make deductions about relatedness difficult.

The second problem that *Ovatus* poses is biogeographical. As currently understood, the genus is Holarctic, with ten species native to Eurasia, and four native to North America. Perhaps, then, comparative species should be drawn from related genera on both continents. Nearly all species of *Myzina*, the subtribe to which *Ovatus* belongs, are endemic to Eurasia, with the subtribe's greatest diversity in southern and eastern Asia. Therefore, choosing Eurasian species for comparison is easy. But examination of the native aphid fauna of North America shows that there are only a handful of *Myzina* native to this continent. These native species are mostly specialized moss and sedge feeders such as *Myzodium* Börner and *Carolinaia* Wilson. There are few other native North American *Myzina* besides the four putative *Ovatus*, and several species of *Hyalomyzus*. In other work (Stoetzel, Miller and Jensen, in preparation), evidence has been found for the monophyly of *Hyalomyzus* Richards of North America. This leaves few North American groups to which the four *Ovatus* could belong.

Thirdly, the four North American species currently placed in *Ovatus* are extremely similar and possess some unique characteristics. For example, they all have siphunculi more or less cylindrical, but slightly expanded apically (Figs. 9–12). Two of the species also tend to have more than three pairs of setae on the cauda, whereas most *Myzina* have two or three pairs. The four North American species also have a distinctive pattern of pentagonal or hexagonal reticulation on their terga in the apterous viviparous fe-

male. These peculiarities make them isolated morphologically from most of the *Myzina* and make the choice of appropriate species for the current analysis more difficult.

Myzus has for a long time been used for a great diversity of species of *Myzina*. This can be illustrated by examining the list of Eastop and Hille Ris Lambers (1976). They list 53 valid species of *Myzus*, and 40 others that were described in *Myzus*, but subsequently transferred to 27 other genera. The range of species included in the genus has varied from one author to another during this century. In North America most workers have dealt with the genus in a broad sense (Mason 1940, Palmer 1952). Mason states that *Myzus* can be recognized among the Macrosiphina in his tribe Aphidini by the convergent frontal tubercles. Thus in his revision of the genus, Mason (1940) included 20 species that are today scattered among six genera. Despite all this modification or restriction of the definition of the genus, *Myzus* still contains a wide array of species and is quite likely polyphyletic. The diversity of species in *Myzus* and the lack of another genus that is clearly related to the four species in question indicate that *Myzus* is the best choice for use in this analysis. *Myzus* provides a wide array of species to which the four endemic North American species might prove to be closely related.

SPECIES INCLUDED IN THE ANALYSES

Included in the analysis were *Ovatus phloxae* and three very similar North American species, *O. leucocrini*, *O. reticulatus*, and *O. valuliae*. For purposes of testing their relationship to Palearctic *Ovatus*, six other *Ovatus* species were studied, including *Ovatus (Ovatoides) inulae*, the only member of its subgenus. These were chosen based on their availability in the collection of the USNM and material obtained on loan. Thus ten of the world's fourteen *Ovatus* species were analyzed. Adequate material of the other Eurasian species currently placed in *Ovatus* was not available.

Ten species of *Myzus* were included,

Table 2. Data matrix used in the cladistic analyses. Question marks indicate missing data, † indicates a 0/1 polymorphism, and a ‡ indicates a 0/2 polymorphism.

	111111111 122222 2	
	123456789012345678	901234 5
<i>H. eriobotryae</i>	00000000000001110	111011 0
<i>H. jussiaeae</i>	00000000100001110	110011 ?
<i>H. mitchellensis</i>	000111010000101110	111011 0
<i>M. ascalonicus</i>	†201†0101010101110	††000 1
<i>M. cerasi</i>	00000000000000000	000000 0
<i>M. certus</i>	0001100†1010101010	000100 1
<i>M. cymbalariae</i>	120100001110001110	010000 1
<i>M. dycei</i>	0000†0001110100110	010110 1
<i>M. hemerocallis</i>	0201100†1000100010	000011 0
<i>M. lythri</i>	000010000000100010	000000 0
<i>M. ornatus</i>	100110000010110110	000110 0
<i>M. persicae</i>	000100021010001010	000100 1
<i>M. varians</i>	000000001010100110	000110 1
<i>O. crataegarius</i>	001100000100000110	111101 1
<i>O. glechomae</i>	100100001000010110	110001 1
<i>O. insitus</i>	001100001100000110	111101 1
<i>O. inulae</i>	011101101000110010	111101 1
<i>O. leucocrini</i>	031100101011102001	000100 1
<i>O. malisuctus</i>	0111000010101001†0	011110 1
<i>O. mentharius</i>	†001000000001†0110	111001 1
<i>O. phloxae</i>	00010000111110201†	0†000† 1
<i>O. reticulatus</i>	030100021011102000	?????0? 1
<i>O. valuliae</i>	1301000010111120C0	000100 1

representing three of four subgenera, and 16% of the world fauna. These species were chosen to represent all possible subgenera, and are all the species of which adequate material was available. Three outgroup species were chosen from North American *Hyalomyzus*. The dataset is shown in Table 2.

CHARACTERS

Apterous viviparae

Head capsule:

1. Anterior setae on dorsum of head capsule: less than 0.5 times basal width of antennal segment III (0); more than 0.5 times basal width of antennal segment III (1).
2. Ornamentation on dorsum of head capsule: spinules or nodules present anteriorly and along margins, smooth in middle posteriorly (0); without spinules or nodules, sometimes with wrinkles (1); spinules or nodules entirely covering

dorsum of head (2); dorsum of head with posterior surface in middle with polygonal reticulation (3) (Figs. 5–8).

3. Venter of head capsule adjacent to eyes: spinulose (0); smooth (1).
4. Ventral tubercles at rear of head capsule: present (0); absent (1).

Antenna:

5. Ratio of processus terminalis to the base of antennal segment VI: greater than 3 (0); less than 3 (1).
6. Venter of antennal segment II: bumpy (0); smooth (1).

Mouth Parts:

7. Pairs of setae on rostral segment III: almost always 2 (0); more than 2 (1).
8. Ultimate rostral segment: longer than hind tarsal segment II (0); shorter than hind tarsal segment II and without accessory setae (1); shorter than hind tarsal segment II and with accessory setae (2).
9. Number of setae on ultimate rostral seg-

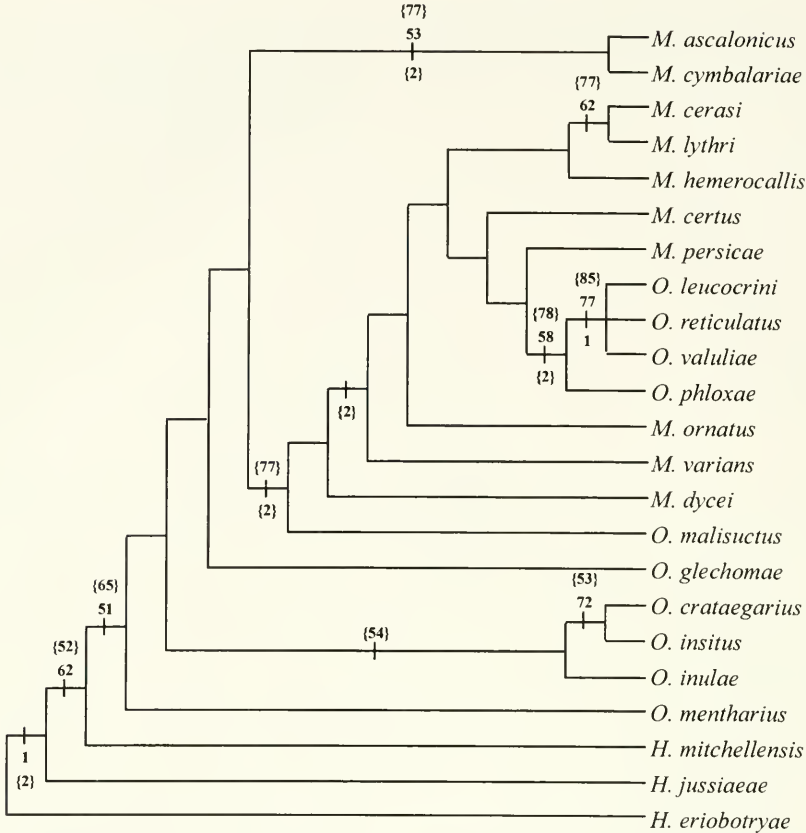


Fig. 1. Tree number one of two equally parsimonious trees found using the heuristic search option in PAUP with successively weighted data (weighted consistency index: 0.67; retention index: 0.84; and rescaled consistency index: 0.57). This tree was also one of 135 trees found using unweighted data (unweighted consistency index: 0.47; retention index: 0.64; and rescaled consistency index: 0.30). Numbers below some branches indicate branch support values from decay analyses, plain numbers indicating unweighted branch support, and numbers in braces indicating rescaled branch support from the weighted data (Bremer 1994). Numbers above branches display results of bootstrap analyses, plain numbers indicating results using unweighted data, and numbers in braces representing weighted data.

ment: 0–3 (usually 2) or rarely 4 accessory setae (0); usually 3 or more (rarely 2) accessory setae (1).

Legs:

10. Dorsal base of hind tibia: smooth or slightly wrinkled (0); distinctly scabrous or imbricated (1).
 11. First tarsal segments chaetotaxy formula: 3–3–3 (0); 3–3–2 (1).

Abdomen:

12. Tergum patterning or sculpturing: maze-like with no distinct polygons, or

irregular closed shapes with smooth space between them (0) (Fig. 3); smooth (1); pentagonal or hexagonal (2) (Fig. 4).

13. Spinal tubercles on abdominal tergite VII: usually present (0); absent (1).
 14. Setae on abdominal tergite VIII: much shorter than basal width of antennal segment III (0); subequal to basal width of antennal segment III (1).
 15. Shape of siphunculi: cylindrical or tapering (0); distinctly swollen (1); very slightly expanded near apex (2).

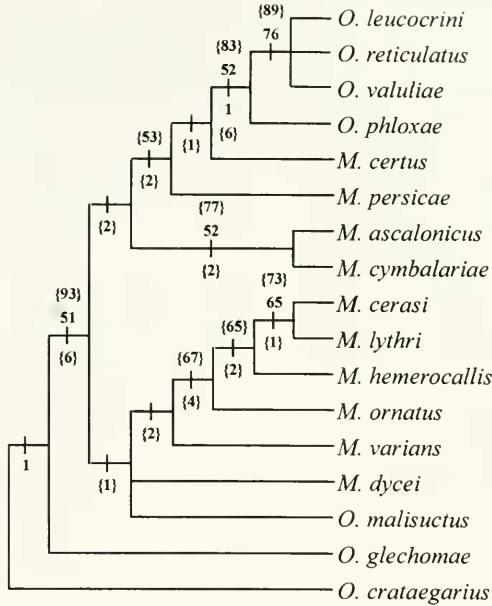


Fig. 2. Tree number one of four equally parsimonious trees found using the heuristic search option in PAUP with successively weighted data (weighted consistency index: 0.77; retention index: 0.84; and rescaled consistency index: 0.65). This tree was one of 14 trees found using unweighted data (unweighted consistency index: 0.47; retention index: 0.64; and rescaled consistency index: 0.30). Numbers below some branches indicate branch support values from decay analyses, plain numbers indicating unweighted branch support, and numbers in braces indicating rescaled branch support from the weighted data (Bremer 1994). Numbers above branches display results of bootstrap analyses, plain numbers indicating results using unweighted data, and numbers in braces representing weighted data.

- 16. Apical spinulation of cauda: entire, without blank spaces dorsally (0); reduced with blank spaces dorsally (1).
- 17. Abdominal tergum pigmentation: pigmented, with complete or nearly complete dorsal shield (0); pale, or with only cross bands on tergites VII and/or VIII.
- 18. Setae on cauda: 2 or 3 lateral pairs (0); 4 or more lateral pairs (1).

Alate viviparae

Antenna:

- 19. Secondary rhinaria on antennal segment V: absent (0); present (1).
- 20. Secondary rhinaria on antennal segment IV: absent (0); present (1).
- 21. Secondary rhinaria on antennal segment III: restricted to approximately half the circumference of the segment

(0); distributed around the entire circumference of the segment (1).

Mouthparts:

- 22. Ornamentation of lateral part of mandible (base of mouthparts): spinulose or scabrous (0); smooth (1).

Abdomen:

- 23. Lateral abdominal tubercles: present in at least some specimens (0); absent (1).
- 24. Pigmented abdominal patch or bands: present (0); absent (1).

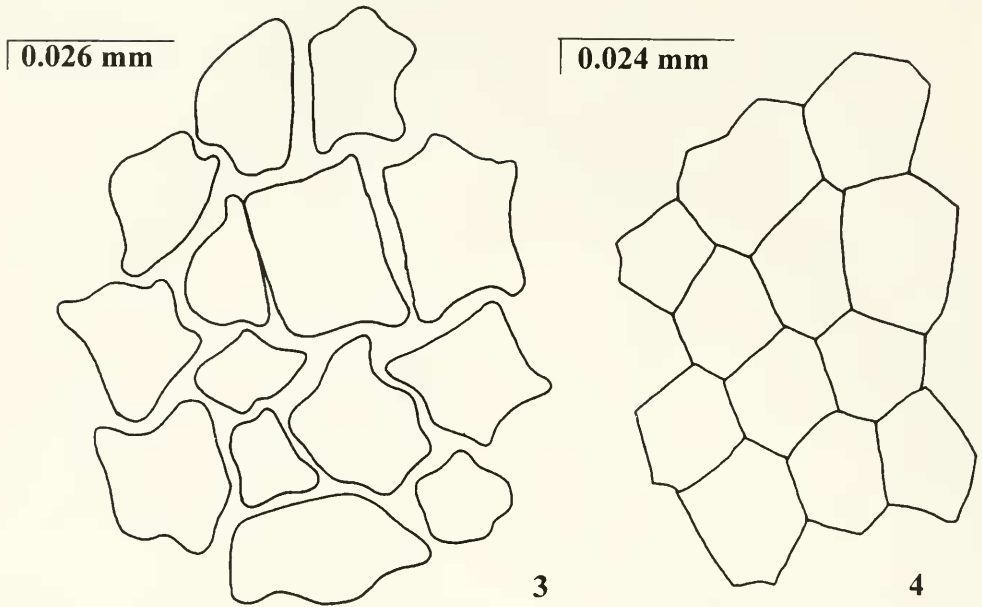
Nymphs

Legs:

- 25. Apical spinulation of hind tibia: present (0); absent (1).

CLADISTICS RESULTS AND DISCUSSION

The full data set was analyzed using the heuristic search option in PAUP. One hun-



Figs. 3, 4. Dorsal sculpturing. 3, *Ovatus crataegarius*. 4, *Abstrusomyzus leucocrini*.

dred iterations of random addition sequence were performed, finding 135 equally parsimonious trees of length 91 steps. These had a consistency index (CI) of 0.47, retention index (RI) of 0.64, and rescaled consistency index (RC) of 0.30. One of these trees is presented in Fig. 1, with numbers below a few branches indicating results of a decay analysis (see Bremer 1994), and numbers above branches indicating the level of bootstrap support from 100 replications of heuristic bootstrap searching. Only branches supported by more than 50% of the bootstrap trees are labeled in Fig. 1. In all 135 trees, the group of four North American *Ovatus* is placed among the *Myzus* species, separate from other *Ovatus*, and supported by more than 50% of the bootstrap trees. Old World *Ovatus* are placed as close relatives to the outgroup *Hyalomyzus*. The close relationship between *Ovatus* and *Hyalomyzus* has been discussed by Eastop (1966), Nielsson and Habeck (1971), and Blackman and Eastop (1994).

The four North American *Ovatus* formed a clade in all 135 trees and were often placed with *M. certus* and *M. persicae*, two

species with swollen siphunculi that represent the subgenus *Nectarosiphon*. Moving the four North American species from within *Myzus* to the more basal parts of the tree along with the other *Ovatus* caused an increase in tree length of three or four steps, depending on the branch to which they were attached. For example, moving the branch composed of these four species to become the terminal *Ovatus*, along with *Ovatus malisuctus* (Matsumura), caused an increase in tree length of three steps. But it is clear from the bootstrap results that the most strongly supported clade of more than two species is that composed of the four North American species related to *O. phlox-ae*, henceforth referred to as the "*phlox-ae* group."

A successive weighting procedure using the default settings in PAUP was conducted, finding two of the 135 trees found using unweighted data, with the following weighted statistics: length, 22, 140; CI, 0.67; RI, 0.84; RC, 0.57. The tree shown in Fig. 1 is one of these trees. Bootstrap and decay analyses were performed using the weighted dataset, and their results are dis-

played in Fig. 1. Decay indices in braces in Fig. 1 are rescaled (Bremer 1994). The two successive weighting trees even more strongly support the monophyly of the *phloxae* group and its separation from Palearctic *Ovatus*. Monophyly of the *phloxae* group was supported in 78% of the bootstrap trees and through 2 rescaled steps of decay.

The results of this analysis clearly indicate that the *phloxae* group does not belong to *Ovatus*. Consistent placement of the *phloxae* group within the clade of *Myzus* species indicates that they are more closely related to *Myzus* than they are to *Ovatus* of the Palearctic. It should also be pointed out that *O. malisuctus* is placed among the *Myzus* clade in some of the 135 trees, and may be more closely related to *Myzus* than are the other *Ovatus*. Further studies focusing on Palearctic aphids in and related to *Ovatus* will be required to finalize the classification of this and other problematic species not included in this study.

The unique characters of the four North American "*Ovatus*" species (peculiar siphuncular shape, generally more setose rostrum and cauda, reticulate tergum) may justify the erection of a new genus. Therefore, another analysis was conducted focusing only on the relationship of these four species to the *Myzus* included in the analysis. The objective of this analysis was to determine whether the *phloxae* group and the available *Myzus* species would form separate monophyletic groups. The same set of characters was used. Three Palearctic *Ovatus* were included, the first two as outgroup taxa: *O. crataegarius*, *Ovatus glechomae* Hille Ris Lambers, and *O. malisuctus*. In-group species were the *phloxae* group, and all ten *Myzus* in the first analysis.

A "branch and bound" search found fourteen trees of length 71, with a CI of 0.55, RI of 0.56, and RC of 0.31. One of these trees is presented in Fig. 2. Similar to the previous analysis, the *phloxae* group is part of a clade with two *Myzus* (*Nectarosiphon*) species. These *Myzus* have swollen

siphunculi and, similar to the *phloxae* group, two setae on the first segment of the hind tarsus. Rearranging the trees to make the *phloxae* group and *Myzus* monophyletic requires only a two step increase in tree length. A successive weighting analysis was conducted, which selected four of the original fourteen trees of length 71 (weighted statistics: length, 19, 611; CI, 0.77; RI, 0.84; RC, 0.65). The tree in Fig. 2 is one of these trees. The results of weighted and unweighted decay and bootstrap (500 replications) analyses are presented in Fig. 2 as well. Unweighted data supported the unity of the *phloxae* group through 1 step of decay and in 52% of the bootstrap trees. Few branches were strongly supported by either measure using unweighted data. Weighted data yielded very strong support for the *phloxae* group, which held up through six steps of rescaled decay and was present in 83% of the bootstrap trees.

These results point to the necessity for the erection of a new genus to house the *phloxae* group. First of all, it is clear that the *phloxae* group is not congeneric with *Ovatus* from the Palearctic. The full analysis that used *Hyalomyzus* as outgroup was overall rather weak, but where it was relatively strong was in the separation between the basal *Hyalomyzus/Ovatus* clade and the more apical *Myzus/phloxae* group clade. This showed that the *phloxae* group is more closely related to *Myzus* than to Palearctic *Ovatus*. The next step in the analysis examined more closely the relationship between the *phloxae* group and the other *Myzus*. The results showed that there was strong support for the monophyly of the *phloxae* group, but not for the relationship between it and the *Myzus* with which it was placed in the trees. Thus not only is there no support for the placement of the *phloxae* group in *Ovatus*, but the group also appears to be only weakly related to any species of *Myzus*. Our cladistic results as well as the peculiar morphology of the *phloxae* group provide ample justification for the erection of a new genus, as we do below.

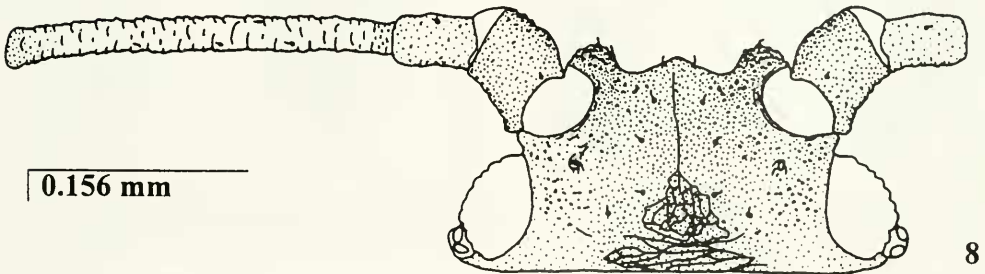
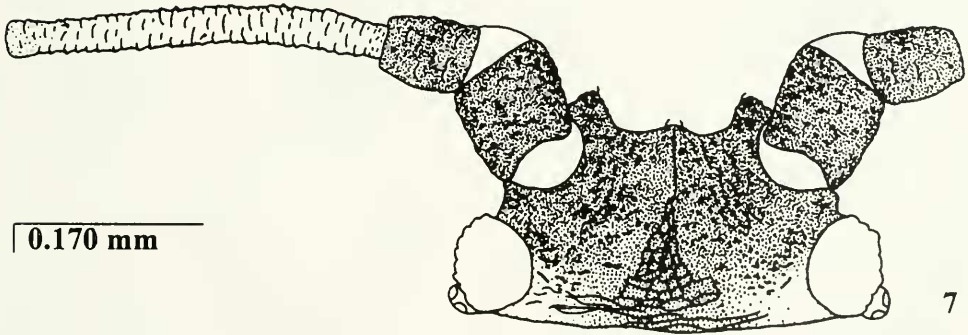
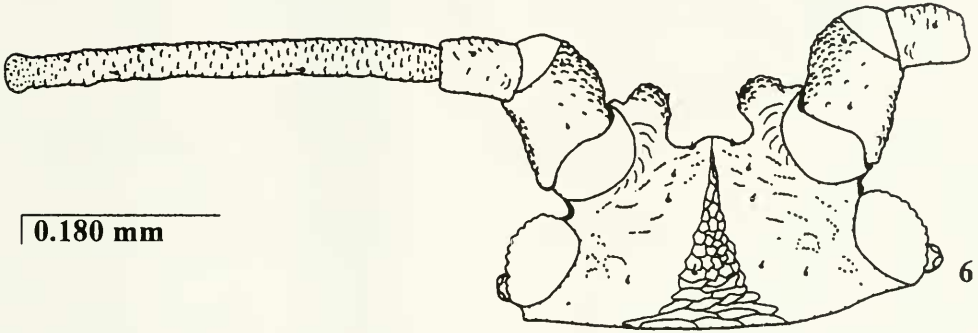
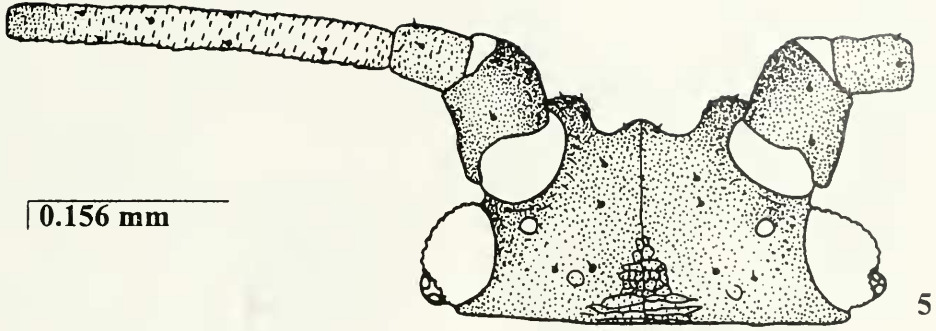
***Abstrusomyzus* Jensen and Stoetzel,
new genus**
(Figs. 4–18)

Type species: *Phorodon phloxae* Sampson

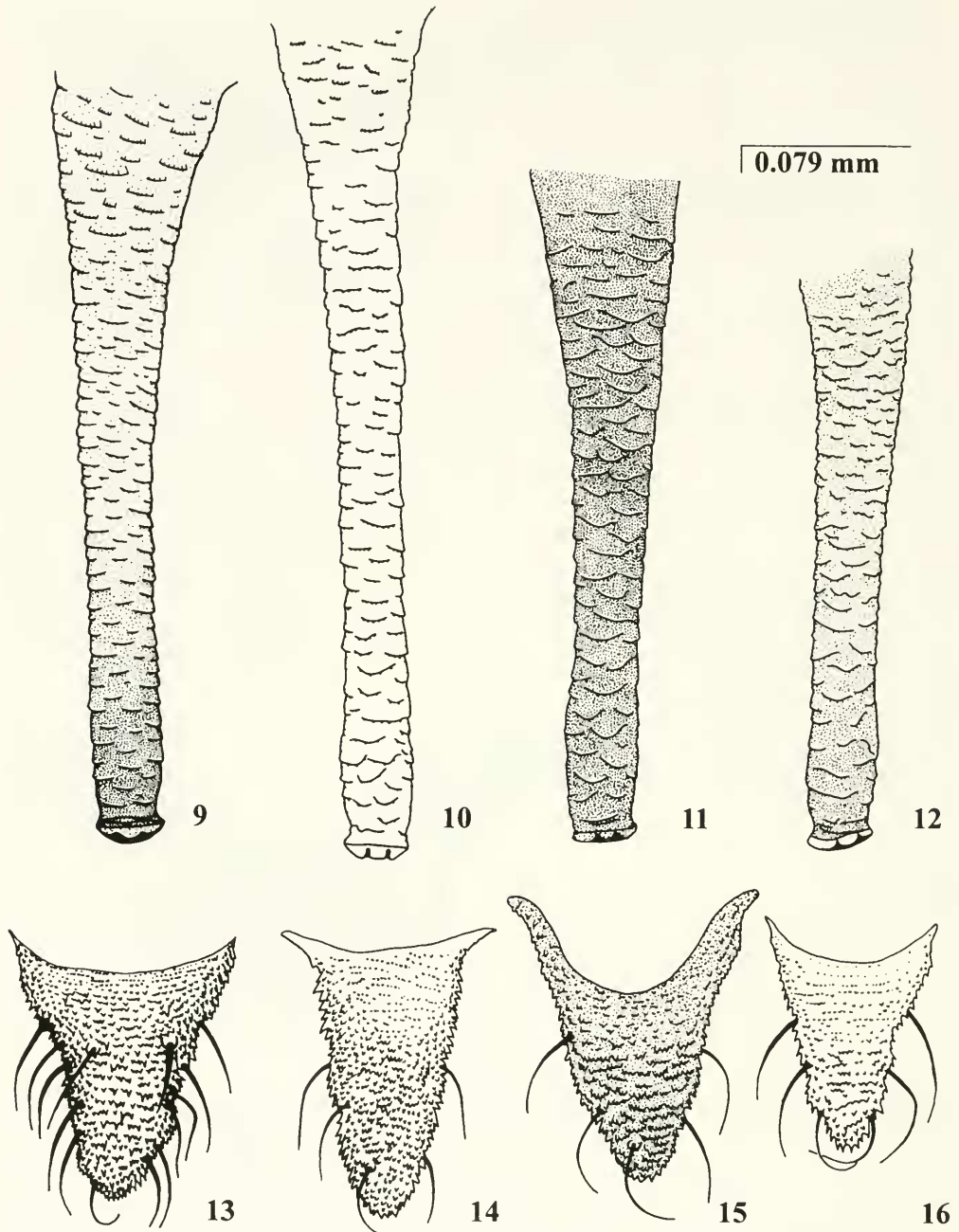
Diagnosis.—*Abstrusomyzus* can be separated from *Ovatus*, *Myzus* and other *Myzus*-like genera in North America by the peculiar shape of the siphunculi in all stages (Figs. 9–12), the distinctly pentagonal/hexagonal reticulated pattern of the tergum (Fig. 4), 3,3,2 first tarsal segment chaetotaxy, and the usual presence of pigmented cross-bands on the abdomen of alate viviparae (Figs. 17, 18). The completely pigmented tergum in apterous viviparae of the three species other than *A. phloxae* is also unusual. One North American species that may be closely related to *Abstrusomyzus* is *Aphthargelia symphoricarpi* (Thomas). The latter species shares with *Abstrusomyzus* the same type of dorsal reticulate sculpturing, moderately prominent *Myzus*-like antennal tubercles, a relatively large number of caudal setae, large lateral tubercles, and dark transverse abdominal bands in the alate viviparae. *Abstrusomyzus* and *A. symphoricarpi* differ significantly, in that the latter species has 3,3,3 first tarsal chaetotaxy, very short almost barrel-shaped siphunculi, and more numerous secondary rhinaria on antennal segments III–V.

Description.—*Apterous vivipara*: Nymph: hind tibiae of nymphs without spinules apically. Adult: body length 0.83–1.94 mm. Dorsum of head capsule (Figs. 5–8) pale to black, with small sparse spinules often arranged in curving rows. Spinal region of head capsule with more or less triangular area of reticulate sculpturing; spinal tubercles sometimes present. Dorsum of head normally with 4 setae in posterior row, with 3 pairs farther forward; small lateral ocelli or traces thereof often present. Antennal tubercles moderately to strongly produced, rough, with several setae. Frons often produced slightly as a median tubercle. Setae on head short, blunt, much shorter than basal width of antennal segment III. Eyes nor-

mal, with ocular tubercles and interfacetal spaces brownish pigmented. Ventral surface of head capsule more or less evenly, but sometimes very lightly, spinulose, with spinules often arranged in rows. Antennal tubercles with large ventral projections bearing a few short setae. Ventral head setae sometimes as short as the dorsal setae, sometimes about twice as long. Mandibular area of mouthparts smooth. Antennae normally shorter than body; antennal segment I rough, roughest medially, with several setae, these about equal in length to those on dorsum of head capsule; antennal segment II rough, roughest ventrally and medially, with course imbrications; antennal segment III covered with imbrications, rarely with 1 or 2 secondary rhinaria; remainder of antenna roughly imbricated. Rostrum reaching middle of thorax, with segment II strongly ornamented with rows of spinules; segment III with 2 pairs of setae, these located in apical $\frac{1}{2}$; ultimate rostral segment about equal in length to tarsal segments II, or about 0.1 mm, with 3–9 accessory setae. Pronotum with 3 pairs of short setae: 1 spinal, 1 pleural, and 1 lateral; the lateral pair associated with a frequently present pair of lateral tubercles that are sometimes bi- or trifid; setae about equal in length to those on the dorsum of the head. Surface of pronotum reticulate, the reticulations usually somewhat flattened front to back. Meso- and metathoracic terga reticulate and often pigmented, setae extremely short, blunt. Coxae of all legs covered with spinulose imbrications. Femora with sparse imbrications, especially anteriorly, with setae about equal in length to dorsal head setae. Tibiae sparsely setose, basal setae much shorter than those at apex. First tarsal segments with 3,3,2 setae (i.e., hind tarsus I with 2 setae), second tarsal segments imbricated. Mesothoracic furca sessile or with short stalk. Abdomen with tergum reticulate throughout, sometimes pigmented. Dorsal abdominal setae blunt, very short, except sometimes longer on tergite VIII. Abdominal segments II–VI often with lateral tu-



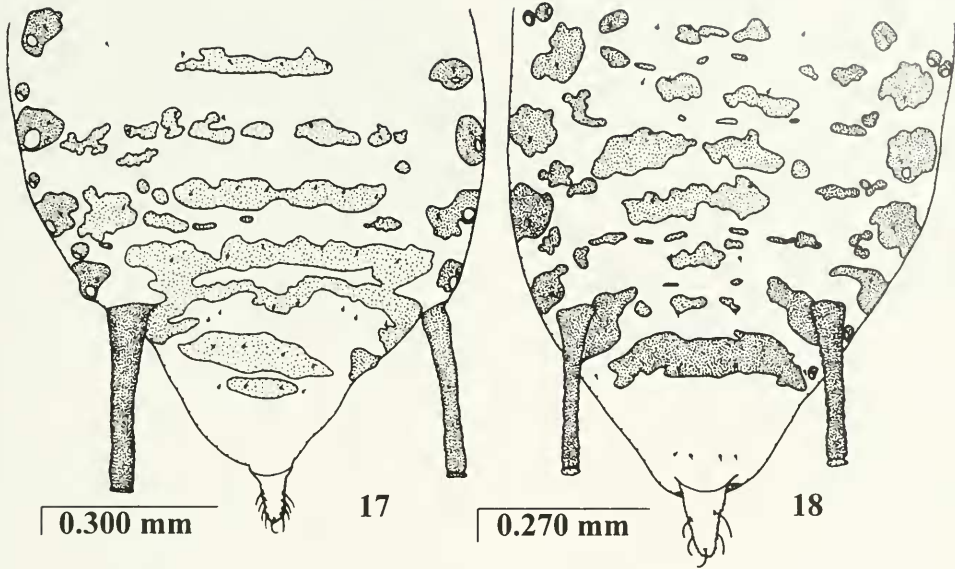
Figs. 5-8. Head with first three antennal segments of apterous viviparae. 5, *Abstrusomyzus leucocrini*. 6, *A. phloxae*. 7, *A. reticulatus*. 8, *A. valuliae*.



Figs. 9-16. Siphunculi and caudae of apterous viviparae. 9, 13, *Abstrusomyzus leucocrini*. 10, 14, *A. phloxae*. 11, 15, *A. reticulatus*. 12, 16, *A. valuliae*.

bercles of various sizes. Siphunculus cylindrical over most of its length, slightly swollen toward the tip (Figs. 9-12), imbricated throughout. Cauda moderately long, with

4-15 setae, more or less pointed apically. Tergite VIII with 4-7 setae, normally 4. Ventral abdominal setae pointed. Gonapophyses 3 in number.



Figs. 17, 18. Abdominal tergum of alate viviparae. 17, *Abstrusomyzus leucocrini*. 18, *A. phloxae*.

Alate vivipara: Body length 0.98–1.92 mm. Head capsule dark, slightly wrinkled or smooth, not reticulate. Lateral and median ocelli present, median ocellus creating a strong median tubercle. Antennal tubercles only slightly rough, with several setae. Ventral surface of head capsule more or less smooth, sometimes with a few sparse spinules. Antennal segment III with secondary rhinaria scattered over most or all of its length, limited to one side, normally less than 20 in number; antennal segment IV occasionally with a few secondary rhinaria; antennal segment V without secondary rhinaria. Thoracic tergites smooth. Sclerites of thorax dark brown, of normal design. Abdomen with dark lateral sclerites, and often dark cross bands on some segments. Dark abdominal cross bands often reticulate in a similar fashion to the tergum of apterous vivipara. Otherwise essentially as in apterous vivipara.

Etymology.—The generic name is taken from the Latin word “abstrusus,” meaning hidden or concealed and *Myzus*, which is based on the Greek “myzo,” meaning suck. The name is meant to draw attention to the

way the type species of the genus is often hidden in ant-created shelters or on the lower leaves of its host plants. The gender is masculine.

KEY TO APTEROUS VIVIPARAE OF
ABSTRUSOMYZUS

1. Dorsum of apterous vivipara unpigmented; antennal tubercles strong, with prominent converging processes (Fig. 6); dorsum with hexagonal reticulation usually faint due to the pale, unsclerotized tergum
 *Abstrusomyzus phloxae* (Sampson)
- Dorsum of abdomen of apterous vivipara dark pigmented, usually black; antennal tubercles strong, but without converging processes (Fig. 5, 7, 8); dorsum with distinct hexagonal reticulation (Fig. 4) 2
2. Apterous vivipara without traces of lateral ocelli, and without spinal tubercles on head; antennal segments I & II nearly black, antennal segment III unpigmented, except extreme tip slightly dusky; dorsum entirely dark, concolorous with cauda and siphunculus
 *Abstrusomyzus reticulatus* (Heie)
- Apterous vivipara usually with traces of lateral ocelli, and sometimes with low spinal tubercles on head; antennal segment I brown, antennal segment II much paler than I, antennal segment III with tip brown; dorsum entirely dark or

- with some pale areas, cauda and siphunculus pigmentation variable 3
- 3. Tergite VIII with middle pair of setae pointed, about twice as long as lateral pair of setae on tergite VIII, and about three times as long as setae on tergite VII; cauda usually with fewer than 9 setae (Fig. 16)
 *Abstrusomyzus valuliae* (Robinson)
- Tergite VIII with middle pair of setae blunt, about equal in length to the lateral pair on tergite VIII and those on tergite VII; cauda usually with more than 9 setae (Fig. 13)
 *Abstrusomyzus leucocrini* (Gillette and Palmer)

KEY TO KNOWN ALATE VIVIPARAE OF
ABSTRUSOMYZUS

- 1. Setae on abdominal tergite VIII distinctly longer than setae on tergite VII, and about equal to basal width of antennal segment III; lateral tubercles small or absent
 *Abstrusomyzus valuliae* (Robinson)
- Setae on abdominal tergite VIII about equal in length to the setae on abdominal tergite VII, and much shorter than the basal width of antennal segment III; lateral tubercles various 2
- 2. Cauda relatively setose, usually with more than 9 setae; lateral abdominal tubercles relatively large (Fig. 17); antennal tubercles moderately prominent as in Fig. 5
 *Abstrusomyzus leucocrini* (Gillette and Palmer)
- Cauda usually with fewer than 9 setae; lateral abdominal tubercles small or absent (Fig. 18); antennal tubercles sometimes strongly produced similar to the apterous vivipara (Fig. 6)
 *Abstrusomyzus phloxae* (Sampson)

Abstrusomyzus leucocrini (Gillette and Palmer 1929), **new combination**
 (Figs. 4, 5, 9, 13, 17)

Myzus leucocrini Gillette and Palmer 1929: 470; Gillette and Palmer 1934: 202; Palmer 1952: 338.

Ovatus leucocrini: Eastop and Hille Ris Lambers 1976: 328; Smith and Parron 1978: 225; Remaudière and Remaudière 1997: 135.

This species was described from several collections made by L.C. Bragg from Fort Collins, Colorado, in May of 1916. The aphids were found on *Leucocrinum montanum*, a small herb of the Liliaceae. We know of no other collections of this aphid

from *Leucocrinum*. There are a few individual alate viviparae found in traps and on various plants that seem to be this species, but lack of good host plant records makes any deductions about the biology of this species difficult. The presence of many apterous and alate viviparae on an herb (*Leucocrinum*) in May suggests a monoecious life cycle. Further collecting will be needed to determine whether this species is monophagous on *Leucocrinum*, or feeds on other plants as well.

Within *Abstrusomyzus*, this species is most similar to *A. reticulatus* and *A. valuliae*. In the material at hand (19 apterous, and 15 alate viviparae), the apterous viviparae of *A. leucocrini* almost always have partially developed lateral ocelli, and often spinal tubercles on the head as well (Fig. 5). *Abstrusomyzus reticulatus* lacks both of these, and *A. valuliae* always lacks the latter, but usually lacks both. The cauda of *A. leucocrini* is usually more setose, ranging from 9–15 setae in both alate and apterous viviparae, compared to 4–9 setae on the cauda (Figs. 13, 15, 16) of the other two species. This species and *A. phloxae* have characteristic brown to orange regions of pigmentation surrounding the bases of the siphunculi. It is not known whether the other two species in the group have this unusual pigmentation pattern. Differences between *A. leucocrini* and *A. phloxae* are discussed under the latter species. Adequate descriptions of this species have been published previously (Mason 1940, Palmer 1952).

Types of this species are located in the USNM. A single paratype slide was also obtained on loan from the BMNH, and another from UCB. Other material examined were specimens from the same series as the types, some of which were cleared and remounted for this study.

Abstrusomyzus phloxae (Sampson 1939), **new combination**
 (Figs. 6, 10, 14, 18)

Phorodon phloxae Sampson 1939: 174.
Myzus plantagineus Passerini (misidentifi-

cation): Williams 1911: 65; Davis 1910: 495; Davis 1911: 23; Mason 1940: 17.

Ovatus phloxae: Hille Ris Lambers 1966: 600; Heie 1972: 450; Eastop and Hille Ris Lambers 1976: 329; Smith and Parron 1978: 225; Remaudière and Remaudière 1997: 135.

Abstrusomyzus phloxae was described from California based on specimens collected on *Phlox subulata*. Sampson described the species in *Phorodon* Passerini under a broad concept of the genus that included species that are today considered *Ovatus* and *Myzus*. Since Sampson (1939), the species has been collected on many other plants (Table 1). In the eastern half of the U.S.A., *A. phloxae* is most often found on the crown, young leaves, and roots of *Plantago major*. This led to the misidentification of this species by Williams (1911) and Mason (1940) as *Myzus plantagineus* Passerini. Hille Ris Lambers (1966) was the first to understand the identity and wide host range of this species.

This species has been found on many unrelated host plants, but mostly only in isolated collections. It has been best studied in eastern U.S.A. on *Plantago major*. It was collected on this plant in Illinois, Maryland, Nebraska, Pennsylvania, and Virginia in May, June, and July of various years. When feeding on this plant *A. phloxae* is often tended by ants (*Lasius alienus* Foerster in Maryland) which build earthen "tents" surrounding the young leaves on which the aphids feed. Such "tents" we found in Maryland housed a mixture of aphids, including *A. phloxae*, *Aphis gossypii*, and *Nearctaphis bakeri* (Cowen). We reared *A. phloxae* on *Plantago* on potted plants indoors. To test acceptance of two host plants used by other *Abstrusomyzus* species, we allowed the population of *A. phloxae* on *Plantago* to increase, and provided *Fragaria* sp. (the host genus of *A. valuliae*) and *Oxalis* sp. (the host genus of *A. reticulatus*) in adjacent potted plants. Many *A. phloxae* individuals attempted to colonize *Fragaria* and *Oxalis*,

but no colonies were established during the two weeks of attempts. The *A. phloxae* population eventually killed its host plants. This bolstered the somewhat weak morphological separation between *A. phloxae* and *A. reticulatus* and *A. valuliae*, since despite the polyphagy of *A. phloxae*, it was unable to colonize the hosts of these two species. The aphids reared on potted plants were heavily parasitized by the aphelinid *Aphelinus asychis* Walker.

Little is known about the life history of this species. It has been collected in every month except October and November. In Maryland the earliest collection was February. In Oregon it is most commonly found in August and September. The single known collection of oviparae was found in Abbotsford, British Columbia on 2 January 1992. Given that males have never been found, and considering that it has been collected almost throughout the year, we suspect that *A. phloxae* is primarily anholocyclic. Concerted collecting efforts during autumn and winter will be required to determine the life history of this species.

When *A. phloxae* is found in nature, it almost always lives on the lower leaves of its host plant, and generally on plants that are low to the ground or have a basal rosette. When reared on potted plants indoors, the aphid thrived on all parts of the plant, but moved to the upper parts only when populations were very large. This propensity for living near the ground, but on many different plant species, suggests that this aphid may be a rare example of a habitat-specific, rather than host-specific aphid. Other examples of this phenomenon are known in the aphids, such as the polyphagous tree feeding aphid *Longistigma caryae* (Harris), which feeds specifically on bark, and *Rhopalosiphum nymphaeae*, which feeds on aquatic herbs.

Chromosome number is often useful as a taxonomic character in aphids. For most species of *Myzus* in which it is known, the chromosome number is $2n = 12$, with a few having $2n = 13$ or 14 . One slide obtained

on loan from the BMNH contains a sample of apterous viviparae of *A. phloxae* that was karyotyped as $2n = 18$ by R.L. Blackman. Karyotyping of the other *Abstrusomyzus* species may show that chromosome numbers will also support the separation of *Abstrusomyzus* from similar *Myzus*-like genera.

Within *Abstrusomyzus*, apterous viviparae of *A. phloxae* are easily recognized by their pale tergum and large, distinctly converging antennal tubercles (Fig. 6). Alate viviparae are far more difficult to separate from other members of the group. The alate form of *A. reticulatus* is unknown. The long middle pair of setae on abdominal tergite VIII is diagnostic for *A. valuliae*. This leaves *A. leucocrini* as the primary species that may be confused with *A. phloxae* in the alate stage. *Abstrusomyzus phloxae* has relatively more prominent antennal tubercles, and usually has fewer caudal setae; *A. phloxae* normally has eight or fewer caudal setae (but sometimes up to 10), compared to 9–13 in *A. leucocrini* (Figs. 13, 14). Many *A. leucocrini* have spinal tubercles on the head, which are always absent in *A. phloxae*. Finally, *A. phloxae* tends to have smaller lateral tubercles, and often fainter or less extensive abdominal pigmentation (Figs. 17, 18). Good descriptions of *A. phloxae* can be found in Sampson (1939) and Mason (1940).

Many paratypes of this species were seen, having been borrowed from the UCB. Other material examined included material from all the host plants and states listed for this species in Table 1. Seventy eight apterous viviparae, and 59 alate viviparae were seen during this study.

Abstrusomyzus reticulatus (Heie 1972),
new combination
 (Figs. 7, 11, 15)

Ovatus reticulatus Heie 1972: 447; Eastop and Hille Ris Lambers 1976: 329; Smith and Parron 1978: 225; Remaudière and Remaudière 1997: 135.

This species was described based on nine specimens collected on *Oxalis ?stricta* in

North Carolina. These specimens are still the only ones known for the species. They include seven apterous viviparae, one ovipara, and one brachypterous male.

Abstrusomyzus reticulatus is apparently monoecious holocyclic based on the occurrence of viviparae, a male, and ovipara together on the herbaceous *Oxalis*. According to Heie (1972) the aphids cause the leaves of *Oxalis* to curl. Further collecting will be required to determine the host range of this species.

This species can be distinguished from *A. phloxae* as described above. *Abstrusomyzus valuliae* is distinct from this species and others in the group because of the long setae on abdominal tergite VIII. *Abstrusomyzus reticulatus* is most similar to *A. leucocrini*. These species can be separated based on the small number of caudal setae in *A. reticulatus*, its complete lack of spinal tubercles on the head, and relatively dark antennal segment II. This is the only species of *Abstrusomyzus* for which the male is known. The brachypterous condition of the single known male is probably aberrant. Heie (1972) provides good descriptions of all known morphs.

Types of this species are housed in the USNM (holotype, one paratype), BMNH (3 apterous vivipara paratypes), C.F. Smith collection (two apterous viviparae, not seen), and in the collection of O.E. Heie (one apterous vivipara and one ovipara, not seen).

Abstrusomyzus valuliae (Robinson, 1974),
new combination
 (Figs. 8, 12, 16)

Myzus valuliae Robinson 1974: 469.

Ovatus valuliae: Eastop and Hille Ris Lambers 1976: 329; Smith and Parron 1978: 226; Remaudière and Remaudière 1997: 135.

Abstrusomyzus valuliae is known only from the material used by Robinson for the description of the species from Manitoba,

Canada. It was collected several times during the summer of 1973 and once in the spring of 1974 on *Fragaria vesca*, wild strawberry. These specimens include many apterous and alate viviparae.

Little is known about the biology of this species. It is most likely monoecious, but host plant range is unknown. When on *Fragaria*, the aphids cause the leaves to curl tightly, and the aphids feed inside the curled leaves (Robinson 1974).

This species can be distinguished from *A. phloxae* as described under that species. Among the three darkly pigmented species of *Abstrusomyzus*, this species can be most easily distinguished by the long middle pair of setae on the abdominal tergite VIII. It is most similar to *A. leucocrini*, both species frequently having lateral ocelli or traces thereof in the apterous vivipara. Robinson (1974) described this species thoroughly.

The holotype of *A. valuliae*, which we did not see, was deposited in the Canadian National Collection, Ottawa. Paratypes were deposited in the Canadian National Collection, BMNH, and the USNM. Many paratypes and some additional material from the same collections were examined for this study.

Status of *Ovatus*

The removal of four species from *Ovatus* leaves only a single species of the genus in North America, *O. crataegarius*. This species can be separated from *Myzus* found in North America by its lack of spinules on the hind tibia of nymphs, the lack of a dorsal pigmented abdominal patch in the alate viviparae, and the presence of many secondary rhinaria on antennal segments III, IV, and V in alate viviparae. *Ovatus crataegarius* can be separated from another somewhat similar species, *Phorodon humuli* (Schrank), by its first tarsal chaetotaxy of 3,3,3, lack of pigmented abdominal patch in the alate viviparae, and its antennal tubercles, which are strongly convergent, but lack the extremely prominent finger-like process of *Phorodon*. The primary way that

Ovatus is separated from *Hyalomyzus* is the swollen siphunculi of the latter genus. An excellent diagnosis for the genus *Ovatus*, as it is understood here, is provided by Heie (1994) (i.e., Heie's diagnosis does not address the characters of the four species here placed in *Abstrusomyzus*).

ACKNOWLEDGMENTS

The authors thank Paul A. Brown (The Natural History Museum, London), David J. Voegtlin (Illinois Natural History Survey, Champaign), Cheryl Barr (University of California, Berkeley), James LaBonte (Oregon State University, Corvallis), and C. K. Chan (Agriculture Canada, Vancouver) for the loan of specimens. The manuscript was improved by the comments of Natalia J. Vandenberg and Michael E. Schauff of the U.S. Department of Agriculture, Systematic Entomology Laboratory, Victor F. Eastop of The Natural History Museum, London, David J. Voegtlin of the Illinois Natural History Survey, and Robert G. Footitt of Agriculture Canada, Ottawa. Identifications of the ants and aphelinids were provided by D. R. Smith and M. E. Schauff, respectively, of the U.S. Department of Agriculture, Systematic Entomology Laboratory.

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